The Neogene history of *Prisogaster* Mörch, 1850 (Gastropoda: Turbinidae) in South America

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ABSTRACT

Prisogaster Mörch, 1850, is the sole genus of the turbinid subfamily Prisogasterinae Hickman and McLean, 1990, and is represented by only one extant species, the western South American *P. niger* (Wood, 1828). Two new fossil species from southern Peru (*P. valenciai* new species and *P. mcleani* new species) extend the record of *Prisogaster* to the middle late Miocene and reveal its turbinine ancestry. A major morphological transformation during the late Pliocene produced the modern taxon, which is heavier and more streamlined than its Mio-Pliocene forebears, and thus probably better suited to the higher energy environments that characterize the present-day Peruvian and Chilean coastline.

INTRODUCTION

Prisogaster Mörch, 1850, has rightly been called "enigmatic" by Hickman and McLean (1990) in their study of trochoidean systematics. The genus has only one species, the extant *Prisogaster niger* (Wood, 1828), a gastropod with a sturdy purple-black shell and calcareous operculum. The species is endemic to western South America and has a fossil record not older than the middle Pleistocene [Herm, 1969; not late Pliocene (Hickman and McLean, 1990)]. Individuals of *Prisogaster* live amongst wave-battered intertidal rocks and tide pools (Marincovich, 1973; Guzman et al., 1998), niches more typically occupied by trochids than turbinids (Hickman and McLean, 1990). Its perplexing suite of characters has led *Prisogaster* to be placed in Phasianellinae Swainson, 1840 (Thiele, 1929; Wenz, 1938), Turbininae Rafinesque, 1815 (Knight et al., 1960), and, most recently, Prisogasterinae (Hickman and McLean, 1990).

This paper describes two new fossil species of *Prisogaster* from southern Peru, *P. stucchii* new species and *P. valenciai* new species. Specimens of the former were found near Sacaco in middle upper Miocene and lower Pliocene well-sorted cross-bedded sandstones. Specimens of the latter were encountered farther south near Chala in upper lower Pliocene or upper Pliocene bioclastic gravels. These new taxa demonstrate a dramatic shift in morphology and niche of the living species, *P. niger*, from its Mio-Pliocene predecessor.

GEOLOGY

The Neogene stratigraphy of forearc basin deposits between Pisco and Camaná (Figure 1) was reviewed by DeVries (1998). Upper Miocene and Pliocene marine strata of the Pisco and La Planchada formations include fine-grained tuffaceous and diatomaceous sandstone, which are attributed to outer shelf environments, and coarse-grained massive tuffaceous sandstone from closer to shore (Muizon and DeVries, 1985). Lying disconformably on crystalline basement rocks are cross-bedded and lenticular bioclastic conglomerates, remnants of littoral

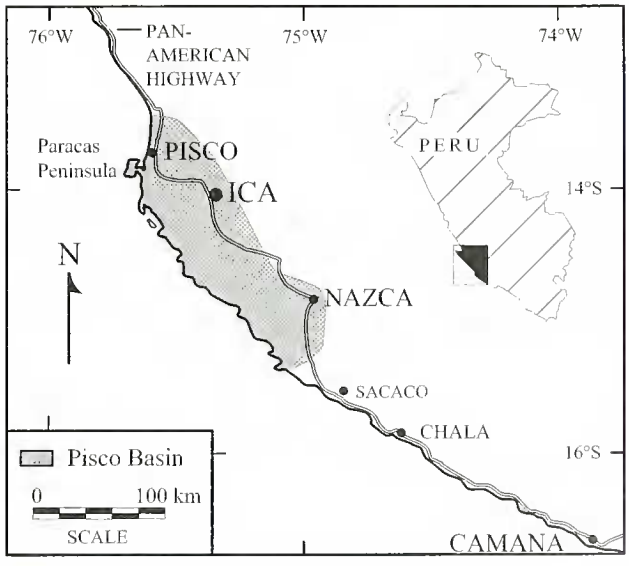

Figure 1. Location of the Pisco forearc basin in southern Peru. New fossil species of *Prisogaster* are from Cenozoic deposits near Sacaco and Chala.

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deposits that lapped onto pre-Eocene erosional platforms or against precipitous Andean foothills. An excellent example of the latter is seen southeast of Chala, where the Panamerican Highway descends in tight curves towards the beach at Playa Huacllaco (Figure 2). Seventy meters of sediment (Figure 3) were deposited in high-energy foreshore and intertidal environments that once flanked rugged cliffs (DeVries, 2003). The age of the Huacllaco beds is constrained by basal beds with specimens of *Concholepas nodosa* Hupé, 1854, *Acanthina triangularis* DeVries, 2003, and *Herminespina mirabilis* (Möricke, 1896), which collectively indicate an early late Pliocene age (DeVries and Frassinetti, 2003), and the uppermost and oldest of several marine terraces, whose 200 m elevation and largely extant taxa suggest a latest Pliocene age (Muizon and DeVries, 1985).

MATERIALS AND METHODS

Specimens described in this study were found by the author. Comparative material was studied at the Los Angeles (California) County Museum of Natural History (LACM). Locality and sample descriptions are listed in the appendix. "DV" locality numbers refer to the author's field notes. Lengths (L) and widths (W) are measured in millimeters. Dimensions of broken specimens are enclosed by parentheses. Figured specimens viewed from oblique angles may be listed with a "maximum viewed width" (m.v. width) measured at right angles to the axis. Some figured specimens are coated with ammonium chloride. Types and numbered specimens are deposited at the Departamento de Paleontología de Vertebrados, Museo de Historia Natural, Universidad de San Marcos, in Lima, Peru (MUSM INV) and University of Washington's Burke Museum of Natural History and Culture in Seattle, Washington (UWBM).

SYSTEMATICS

Family Turbinidae Rafinesque, 1815
Subfamily Prisogasterinae Hickman and McLean, 1990

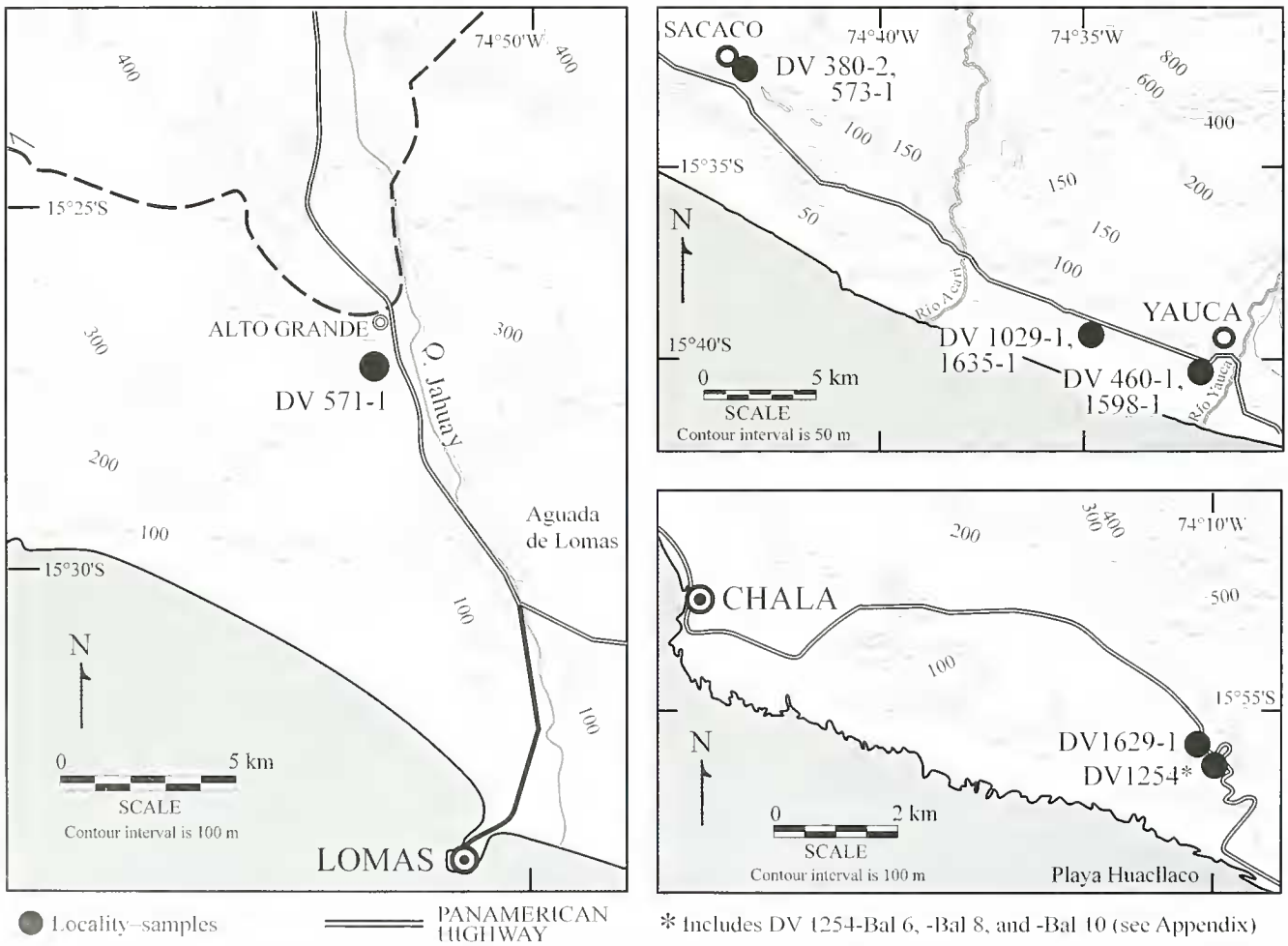


Figure 2. Type localities of *Prisogaster valenciai* new species (locality-samples DV 1254-Bal 6, Bal 8, and Bal 10) and *P. stucchii* new species (DV 571-1). Also shown are lower Pliocene locality-samples near Yauca (DV 1029-1, DV 1635-1, DV 460-1, DV 1598-1) and Sacaco (DV 380-2, DV 573-1) with *P. mclcani* and an upper Pliocene/lower Pleistocene marine terrace southeast of Chala with *P. niger* (DV 1629-1).

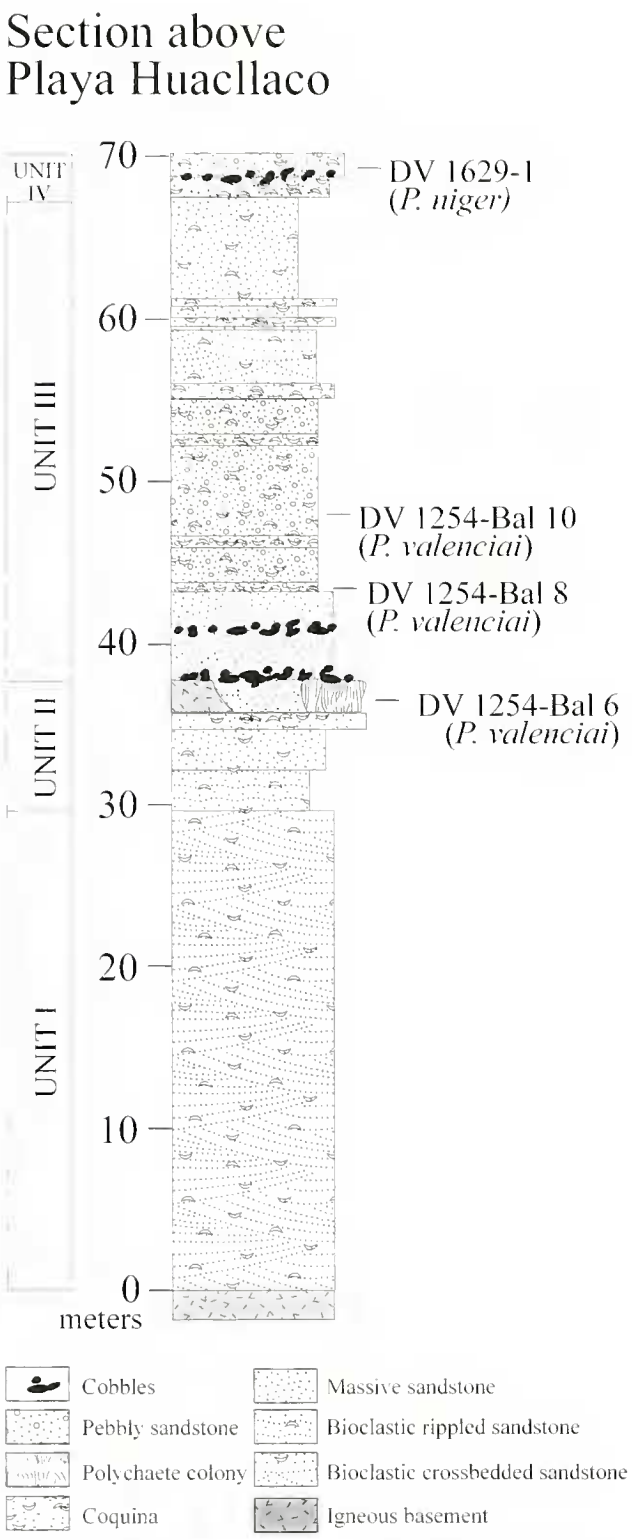


Figure 3. Huacllaco section southeast of Chala with stratigraphic position of type specimens of *P. valenciai* new species and other horizons with *Prisogaster* material.

Genus *Prisogaster* Mörch, 1850

Amyxa F. H. Troschel, 1852 (objective synonym)

Type species: *Turbo niger* Wood, 1828. Type locality not specified.

Discussion: Mörch (1850, p. 21) did not describe *Prisogaster*, but simply applied the new genus name without comment to *Turbo niger* Gray (= *Turbo niger* Wood, 1828), itself introduced with only a drawing and one-word description, "black" (Wood, 1828, p. 18). Hickman and McLean (1990) implicitly defined *Prisogaster* by their description of Prisogasterinae. Diagnostic non-anatomical characters include an incomplete peristome (also present in Turbininae) and an operculum with a "thick, convex exterior calcareous pad" (Hickman and McLean, 1990, p. 52). Other distinguishing shell characters included the black color of the outer shell layer, an oblique aperture, the absence of an umbilicus in adult specimens, a predominance of spiral sculpture, and an inner nacreous layer. New fossil data show that the black color is not diagnostic of the entire genus. The morphology of the operculum is distinctive for the subfamily and genus, however, as is the quadripartite structure of the columella described in this paper.

Prisogaster niger (Wood, 1828)
(Figures 4–10, 13, 14)

Turbo niger Wood, 1828, p. 18, pl. 6, fig. 1; d'Orbigny, 1840, 5: 411–412, vol. 9 (Mollusca), pl. 55, figs. 9–11.

Turbo niger Gray, 1839, p. 143, pl. 36, fig. 1; Hupé, 1854, p. 140.

Turbo (Prisogaster) niger Wood.—Dall, 1909, p. 238.

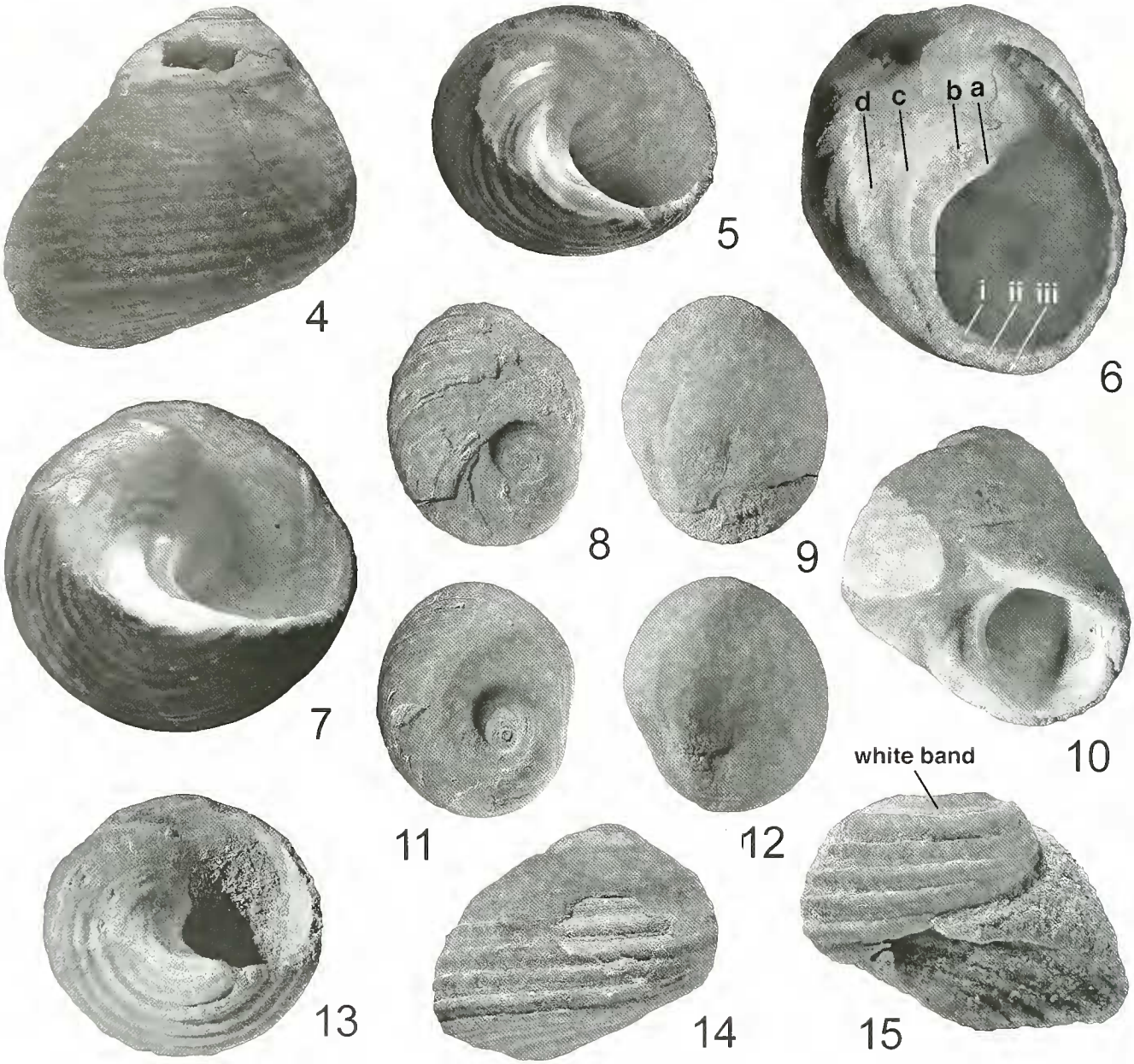
Prisogaster niger Wood.—Mörch, 1850, p. 21; Carcelles and Williamson, 1951, p. 268; Dell, 1971, p. 197; Marincovich, 1973, p. 24, fig. 41; Osorio et al., 1979, p. 18, fig. 15; Ramírez, 1981, p. 130, fig. 154; Alamo and Valdivieso, 1997, p. 15, fig. 30; Guzmán et al., 1998, p. 37, fig. 27; Forcelli, 2000, p. 64, fig. 102; Aldea and Valdovinos, 2005, p. 390, fig. 8-11.

Prisogaster niger minor Mörch, 1850, p. 21.

Trochus gaudichaudii Hupé, 1854, p. 146, Malacologia, pl. 4, figs. 4, 4a, 4b.

Diagnosis: Spiral cords and interspaces purple-black. Whorls slightly angulate anteriorly. Spiral sculpture of 13 to 24 primary spiral cords, including six to ten cords on base.

Description: Shell thick, up to 30 mm long, globose, variably compressed axially. Spire variably elevated, about one-quarter to one-third of shell length. Protoconch unknown; teleoconch with about five whorls. Whorls broadly rounded posteriorly, very weakly angulate or biangulate anteriorly; periphery anterior to axial midpoint of body whorl. Sutures usually appressed, sometimes slightly impressed. Exterior purple-black, spire usually corroded, nacreous. Axial sculpture absent. Spiral sculpture of 13 to 24 primary spiral cords, including six to ten on base; cord widths vary irregularly two-fold. Most posterior spiral cord wider, flatter, forming collar against preceding whorl. Interspaces narrower



Figures 4–15. *Prisogaster* spp. **4–10.** *Prisogaster niger* (Wood, 1828). **4.** UWBM 97829, Pisco Bay, Recent, abapertural view, length = 18.4 mm. **5.** UWBM 97830, Pisco Bay, Recent, oblique basal-apertural view, m. v. width = 15.7 mm. **6.** MUSM INV 116, DV 1629-1, latest Pliocene, oblique basal-apertural view showing quadripartite structure of columella, m. v. width = 17.9 mm. a = inner white column, b = medial nacreous band, c = outer white sinuous ridge, d = outermost elongate excavation, i = inner nacreous layer, ii = middle shell layer, iii = outer purple-black calcitic layer. **7.** UWBM 97829, basal view, width = 19.1 mm. **8.** UWBM 97837, DV 1629-1, operculum, interior view, length = 8.9 mm. **9.** UWBM 97837, operculum, exterior view. **10.** UWBM 97828, DV 398-1, Recent, apertural view showing outer layer and inner nacreous layer on body whorl, length = 18.3 mm. **11, 12.** *Prisogaster mcleani* new species. Early Pliocene. **11.** UWBM 97848, DV 573-1, operculum, interior view, length = 8.7 mm. **12.** UWBM 97848, exterior view. **13, 14.** *Prisogaster niger* (Wood, 1828). **13.** UWBM 97831, DV 461-1, latest Pliocene, basal view, m.v. width = 18.9 mm. **14.** UWBM 97831, abapertural view, length = 16.3 mm. **15.** *Prisogaster valenciai* new species. Late Pliocene. UWBM 97838, holotype, DV 1254-Bal 8, apertural view, width = 15.9 mm.

than spiral cords, shallow, sometimes crossed by strongly prosocline colabral growth-line lamellae. Aperture oblique, diagonally ovate, with incomplete peristome. Umbilicus absent in juveniles and adults. Outer lip thick, strongly prosocline, with weak inflection posteriorly and salient adjacent to suture; inner edge smooth, nacreous. Parietal and umbilical areas weakly excavated, nacreous; sometimes with weak anal canal without sinus. Columella with innermost white column ending anteriorly at slight inflection near columellar base; medially with slightly ex-

cavated, curved, nacreous band alongside innermost columella, narrowing anteriorly, then broadening at base of aperture to join nacreous inner layer of outer lip; also with weakly sinuous white ridge outboard of nacreous band, extending to base of aperture and coalescing with interspace between second and third basal spiral cord to form a blunt tooth; first tooth separated from second blunt tooth abaxially by short groove inside aperture; and with shallow, white, elongate excavation bordering ridge at outer margin of columellar area.

OPERCULUM: Exterior convex, steeper posteriorly and adaxially; basal rim smooth, remainder of surface pustulose, more so peripherally than centrally. Two subaxially elongate, adaxially-anteriorly converging creases on adaxial side of diagonal bulge, inner crease extending to abaxial posterior corner; sinuous growth lines present on abaxial side. Interior nearly planar, coiled, changing from multispiral to paucispiral; all coils with long growing edge. Subsurface texture reticulate with elongate "cells" perpendicular to growth lines.

Material Examined: MUSM INV 113, DV 461–1, latest Pliocene, L 13.6, W 15.6; MUSM INV 114, DV 464–1, middle Pleistocene, L 22.8, W 22.0; MUSM INV 115, DV 463–1, late Pleistocene, L (21.7), W 25.7; MUSM INV 116, DV 1629–1, latest Pliocene, L 15.3, W 17.9; MUSM INV 117, DV 1629–1, L 12.7, W 14.1; UWBM 97828, DV 398-1, Recent, L 18.3, W 17.4; UWBM 97829, Pisco Bay, Recent, L 18.4, W 19.1; UWBM 97830, Pisco Bay, Recent, L 14.6, W 15.1; UWBM 97831, DV 461-1, L 16.3, W 18.5; UWBM 97832, DV 464-1, L 21.0, W 21.6; UWBM 97833, DV 463-1, L (23.5), W 27.0; UWBM 97834, DV 720-1, Holocene, operculum, L 5.1, W 4.4; UWBM 97835, DV 1629-1, L 16.0, W 19.1; UWBM 97836, DV 1629-1, L 13.5, W 14.2; UWBM 97837, DV 1629-1, operculum, L 8.9, W 7.1. DeVries collection: Ipun, Chile, Recent, lot of one; Caldera region, northern Chile, from eight meters deep on sand and rocks, Recent, lot of two; DV 461-1, lot of two; DV 463-1, lot of six; DV 720-1, lot of twelve; DV 730-1, Holocene, lot of one and one operculum; DV 1252-1, latest Pliocene, lot of 3.

Distribution: Ecuador (7°N) to northern Peru: LACM collections, Recent. North-central Peru: Holocene, Recent. Southern Peru: latest Pliocene, early Pleistocene, middle Pleistocene, late Pleistocene, Recent. Chile: middle Pleistocene to Recent (Herm, 1969; Valdovinos, 1999).

Remarks: Modern specimens of *Prisogaster niger* vary in the number of spiral cords and height of the spire. The oldest specimens of *P. niger* from southern Peru have only 13 to 15 primary spiral cords between the columella and suture (e.g., Figures 13, 14), about as few as the youngest specimen of the older *P. valenciai*. Specimens of *P. niger* differ from those of *P. valenciai* by lacking any vestige of cream-colored banding of cords or interspaces.

The modern range of *Prisogaster niger* extends from 7° N to 41° S (LACM collections) and beyond to the Straits of Magellan (Osorio et al., 1979; Valdovinos, 1999), a distribution more extensive than ascribed to the species by Dall (1909) or Alamo and Valdivieso (1997). The Pleistocene record is limited to southern Peru and Chile, with no records from the marine *tablazos* of northern Peru (DeVries, 1986). The late Pliocene record is still more restrictive, with only southern Peruvian specimens known, including the oldest, which were found southeast of Chala (DV 1629-1) in the uppermost coquina (Unit IV) of the Huacllaco section (Figure 3), a shell bed dominated by thick disarticulated valves of the bivalve, *Mulinia edulis* (King, 1831).

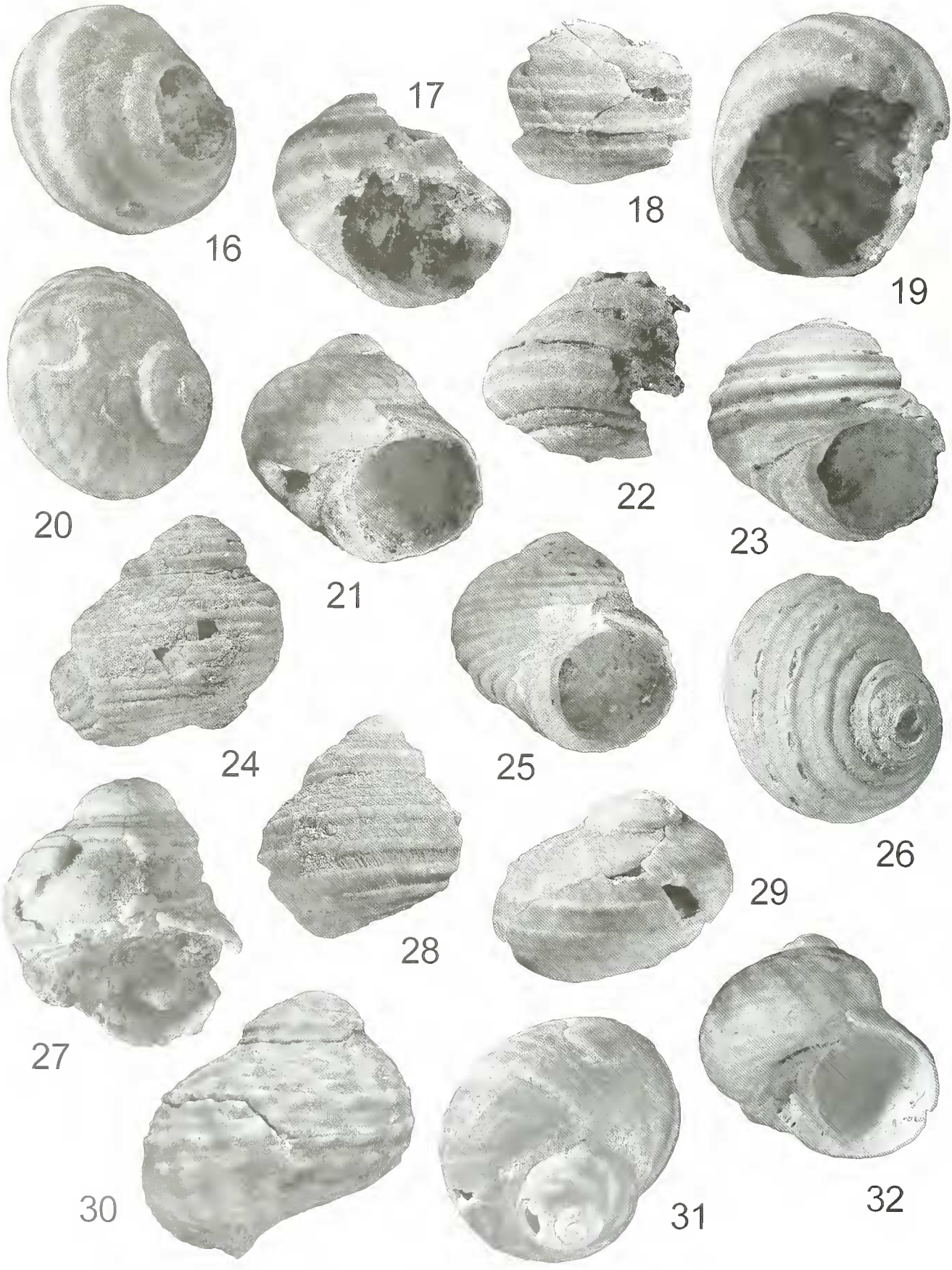
A second modern species assigned to *Prisogaster* has been the Chilean *P. elevatus* (Eydoux and Souleyet, 1852) (Souleyet, 1852, v. 2, p. 594, pl. 37, figs. 15–19; Nicosia and Gaete, 2003). The original figures of "*Turbo elevatus*," however, show a specimen with a blotchy purple-black color, elevated spire, absence of spiral sculpture, wavy growth lines, and evenly convex calcareous operculum visibly coiled on both sides, all features characteristic of *Tricolia* Risso, 1826 (Hickman and McLean, 1990), more particularly the Chilean *Tricolia mcleani* Marincovich, 1973. Neither the 14 mm length of Eydoux and Souleyet's "*Turbo elevatus*," however, nor the deep lunate columellar/parietal excavation, is characteristic of Chilean *Tricolia*, but rather suggest the Chilean trochid, *Diloma nigerrima* (Gmelin, 1791). The generic assignment of "*Turbo elevatus*" remains in doubt.

Prisogaster valenciai new species
(Figures 15–19, 22)

Diagnosis: Compressed axially; sculpture of five to 14 broadly rounded charcoal-gray primary spiral cords, including two to four on the base; one or more interspaces cream-colored.

Description: Shell less than 15 mm long, globose, compressed axially. Thickness indeterminate (inner shell layers missing). Spire moderately elevated, length indeterminate (much of spire missing). Protoconch and early whorls of teleoconch unknown. Whorls broadly rounded posteriorly, weakly angulate anteriorly. Periphery usually anterior to axial midpoint of whorl. Sutures slightly impressed. Exterior gray to black, with interspaces sometimes cream-colored. Axial sculpture absent. Spiral sculpture of five to 14 broadly rounded primary cords, three to 10 posterior to base, two to four on base; spiral cords about equally wide except for broader, flatter, most posterior spiral cord forming low collar adjacent to suture. Interspaces usually narrower than spiral cords, sometimes filled with single secondary spiral cord. Strongly prosocline growth lines, sometimes lamellate. Aperture oblique, diagonally ovate. Outer lip strongly prosocline. Columella and umbilical area missing. Operculum unknown.

Type Material: UWBM 97838, DV 1254-Bal 8, holotype, late Pliocene, L (13.3), W 15.9; UWBM 97839, paratype, DV 1254-Bal 6, L (13.8), W 15.5; MUSM INV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118, paratype, DV 1254-Bal 8, fragment; MUSM INV 119, paratype, DV 1254-Bal 10, fragment.

Type Locality: Roadcut along the Panamerican Highway, 10 km southeast of Chala. Locality-samples DV 1254-Bal 6, DV 1254 Bal-8, DV 1254-Bal 10, late Pliocene, in section at 35, 42, and 47.5 meters, respectively, above crystalline basement (Figures 2, 3), 15°52′ S, 74°10′ W (Chala 1:100,000 quadrangle).

Other Material Examined: UWBM 97840, DV 1031-1, late early Pliocene, L (12.2), W 13.0.

Distribution: Southern Peru: late early Pliocene to late Pliocene.

Etymology: Named in honor of Dr. Niels Valencia Chacón, director of the Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru.

Remarks: The incomplete specimens of *Prisogaster valenciai* preclude a complete description, but the shape, size, and spiral sculpture clearly mark them as examples of *Prisogaster*. These specimens differ from *P. niger* by having one or more cream-colored interspaces and generally fewer and more clearly differentiated primary spiral cords. The oldest known specimen of *P. valenciai* is from the Pliocene section above Playa Huacllaco (Unit II, DV 1254-Bal 6); it has several broad dark spiral cords alternating with cream-colored bands that sometimes encompass a spiral cord and interspace (Figures 18, 22). A specimen from several kilometers away (DV 1031-1) has very few spiral cords, all gray, and equally wide interspaces, all cream-colored (Figures 16, 17, 19).

Most specimens of *Prisogaster valenciai* were found in Unit II and the lower part of Unit III of the Huacllaco section (DV 1254; Figure 3) in cobbly barnacle-rich bioclastic gravel and poorly sorted coarse-grained sandstone thought to have been deposited intertidally or at very shallow subtidal depths. Associated mollusean taxa include *Acanthina* spp; *Concholepas* spp.; *Choromytilus chorus* (Molina, 1782); and a new species of *Xanthochorus* Fischer, 1884 (DeVries, 2005a).

Prisogaster mcleani new species
(Figures 11, 12, 20, 21, 23–32)

Diagnosis: Globose, whorls broadly rounded anteriorly and posteriorly; tan-colored, often mottled, striped, or speckled with brown.

Description: Shell globose, about 20 mm long. Spire moderately to greatly elevated, about 30% to 40% of shell length. Protoconch unknown, teleoconch with about five whorls. Whorls convex, broadly rounded posteriorly and anteriorly, without anterior angulations. Sutures variably impressed. Exterior tan, often with mottling, prosocline flammules, or zig-zag patterns of brown. Axial sculpture absent. Spiral sculpture of ten to 15 rounded primary spiral cords between suture and umbilical area, subdued on smooth specimens; secondary spiral cords rarely interspersed. Entire surface often with tertiary spiral threads. Interspaces variably wide, crossed by strongly prosocline, colabral growth-line lamellae. Juveniles with three weaker spiral cords on base, four to five primary spiral cords on whorl. Aperture oblique, ovate to nearly circular, peristome incomplete. Umbilicus absent. Outer lip thin, strongly prosocline, inner edge smooth. Parietal and umbilical areas weakly excavated in adults. Columella with inner white column curving anteriorly; with a narrow, slightly excavated, nacreous band merging anteriorly with nacre-lined aperture; with a white ridge, slightly sinuous, outboard of the nacreous band, extending to base of aperture and coalescing with interspace between second and third basal spiral cords, with one or two short teeth abaxial; and with an outermost, narrow, white, excavation bordering the ridge at the outer margin of the columellar area, extending anteriorly just over half the length of columella.

Operculum: Exterior convex, steeper posteriorly and adaxially; basal rim smooth, remainder of surface pustulose, more so peripherally than centrally. Two sub-axially elongate, anteriorly converging creases on adaxial side of diagonal bulge, inner crease extending to abaxial posterior corner; sinuous growth lines present on abaxial side. Interior nearly planar, coiled, multispiral changing to paucispiral; all coils with long growing edge. Larger coils with centered shallow, broad, flat-bottomed channel. Subsurface texture reticulate with elongate "cells" perpendicular to growth lines.

Figures 16–32. *Prisogaster* spp. **16–19.** *Prisogaster valenciai* new species. Late Pliocene. **16.** UWBM 97840, DV 1031-1, early late Pliocene, oblique spire view, width = 13.0 mm. **17.** UWBM 97840, apertural view. **18.** UWBM 97839, paratype, DV 1254-Bal 6, abapertural fragment, m. v. width = 12.7 mm. **19.** UWBM 97840, oblique basal-apertural view, m. v. width = 12.4 mm. **20, 21.** *Prisogaster mcleani* new species. **20.** MUSM INV 121, DV 1598-1, early Pliocene, oblique spire view showing change in color pattern and repaired break, m. v. width = 12.1 mm. **21.** MUSM INV 121, apertural view showing naticid drillhole to left of columella, width = 11.5 mm. **22.** *Prisogaster valenciai* new species. Late Pliocene. UWBM 97839, oblique basal view, m. v. width = 12.7 mm. **23–32.** *Prisogaster mcleani* new species. **23.** UWBM 97841, DV 571-1, holotype, middle late Miocene, apertural view showing quadripartite structure of columella (see text), length = 13.9 mm. **24.** UWBM 97842, DV 571-1, paratype, abapertural view, length = 21.1 mm. **25.** MUSM INV 120, DV 1598-1, apertural view showing quadripartite columella and prosocline color stripes, length = 12.4 mm. **26.** UWBM 97841, oblique spire view, m. v. width = 16.5 mm. **27.** UWBM 97842, abapertural view. **28.** UWBM 97844, DV 1598-1, abapertural view of juvenile showing bicarinate whorls and colabral growth-line lamellae, length = 9.4 mm. **29.** MUSM INV 124, DV 573-1, early Pliocene, abapertural view showing flecked stripes, length = 12.7 mm. **30.** MUSM INV 125, DV 571-1, abapertural view showing brown zig-zag pattern, length = 17.8 mm. **31.** UWBM 97843, oblique spire view, m. v. width = 19.7 mm. **32.** UWBM 97843, apertural view, length = 17.9 mm.

Type Material: UWBM 97841, DV 571-1, holotype, middle late Miocene, L 13.9, W 15.4; UWBM 97842, DV 571-1, paratype, middle late Miocene, L 21.1, W (18.5); UWBM 97843, DV 571-1, paratype, L 17.9, W 19.5.

Type Locality: Alto Grande, about one km south of intersection with abandoned paved road to San Juan de Marcona (= El Jahuay locality of Muizon and DeVries, 1985). Shell banks on south-facing slope, 15°26′57″ S, 74°52′06″ W (Acarí 1:100,000 quadrangle).

Material Examined: MUSM INV 120, DV 1598-1, L 12.4, W 12.1; MUSM INV 121, DV 1598-1, L 11.1, W 11.5; MUSM INV 122, DV 1635-1, early Pliocene, L 9.4, W 11.0; MUSM INV 123, DV 460-1, lot of two; MUSM INV 124, DV 573-1, L 12.7, W 14.5; MUSM INV 125, DV 571-1, L 17.8, W 16.0; UWBM 97844, DV 1598-1, early Pliocene, L 9.4, W 8.2; UWBM 97845, DV 1598-1, L 12.1, W 12.7; UWBM 97846, DV 460-1, early Pliocene, L 8.9, W 10.3; UWBM 97847, DV 573-1, early Pliocene, L 12.0, W 13.0; UWBM 97848, DV 573-1, operculum, L 8.7, W 7.8. DeVries collection: DV 1598-1, lot of four; DV 423-3, middle Pliocene, lot of two; DV 1029-1, early Pliocene, lot of two; DV 806-1, late Miocene, lot of one; DV 380-2, early Pliocene, lot of one.

Distribution: Southern Peru: middle late Miocene, early Pliocene.

Etymology: Named after James H. McLean, malacologist, Natural History Museum of Los Angeles County.

Remarks: Specimens of *Prisogaster stucchii* differ from those of *P. niger* by being uncompressed axially, by having an outer calcitic layer that is tan, sometimes with brown mottling and prosocline axial stripes, and by having spiral cords that are narrower and higher, with broader interspaces. The complex structure of the columella, however, is identical with that of *P. niger*, as is the operculum. *Prisogaster mcleani* exhibits considerable variation in spiral ornamentation, with specimens from the same horizons being alternatively densely sculptured with 15 spiral cords (Figures 24, 30), moderately sculptured with eight primary and two secondary cords (Figure 26), and lightly sculptured with ten subdued cords that barely rise above the neighboring wide interspaces (Figures 31, 32). Some Miocene and lower Pliocene juvenile specimens (Figures 28) have a pronounced biangulate profile produced by two strong primary spiral cords posterior to the suture, a feature shared with juveniles of many turbinine species (Hickman and McLean, 1990).

The oldest specimens of *Prisogaster mcleani* were found near Alto Grande (DV 571-1) in middle upper Miocene beds with an estimated age of about 9 Ma (Muizon and DeVries, 1985). Lower Pliocene specimens from Sacaco (DV 380-2) and Yauca (DV 1598-1, DV 1635-1) are identical with the Miocene specimens.

DISCUSSION

The extant *Prisogaster niger*, which appeared about two million years ago, has changed little in either its pattern of low rounded spiral cords or its uniformly purple-black color. *Prisogaster mcleani*, in contrast, resident on southern Peruvian coasts from 9 Ma to 3 Ma, has highly variable spiral sculpture and coloration. Some specimens (Figures 24, 28, 30) exhibit the high spires, impressed sutures, numerous primary spiral cords, and bicarinate juvenile whorls that characterize many members of Turbininae. These similarities strengthen the case of Hickman and McLean (1990) that Prisogasterinae and Turbininae are sister taxa and that *Prisogaster* arose from an advanced turbinine.

Prisogaster probably appeared in southern Peru during the early late Miocene, since no turbinines have been found in middle Miocene or older beds in southern Peru. Its arrival coincided with that of other taxa that constituted the core of a late Miocene-early Pliocene molluscan fauna in southern Peru and northern Chile (DeVries, 2002). The route by which *Prisogaster* or its predecessor arrived in Peru is unclear. No medium-sized or large turbinids are known from Miocene deposits of Chile (Philippi, 1887; Tavera, 1979; Nielsen et al., 2004). The only Miocene turbinid from northern Peru (Spieker, 1922) is probably related to two northern Peruvian Recent species of *Turbo* (*Taeniaturbo*) Gray, 1850; the modern species have opercula with strong and complex external spiral relief very unlike the sculpture on the opercula of fossil and Recent species of *Prisogaster*. The pustulose convex opercula and multipartite columellae of some species of *Turbo* (*Marmarostoma*) Swainson, 1829, do resemble those of *Prisogaster*, although opercula of the former are more broadly convex and not scored by diagonal grooves, and the columellae of the shell do not have a well differentiated ridge and groove structure toward the perimeter of the columellar area. Modern species of *Turbo* (*Marmarostoma*) have an Indo-Pacific distribution, suggesting that *Prisogaster* might be a trans-Pacific immigrant, as other western American taxa have been (Emerson, 1978), including, it appears, the trochid species, *Diloma nigerrima* (Gmelin, 1791) (Donald et al., 2005).

The transition from the globose tan-colored and brown-mottled *Prisogaster mcleani* to the axially compressed purple-black *P. niger* occurred during the time represented by Units II and III of the Huacllaco section (Figure 3), i.e., latest early Pliocene to late Pliocene, in the guise of *P. valenciai*. The oldest specimen of *P. valenciai* (Figures 18, 22; DV 1254-Bal 6) show the first appearance of broad black spiral cords and the persistence of thin cream-colored interspaces, the latter of which become relegated to spire whorls on the youngest specimens (Figure 15; DV 1254-Bal 10).

The late Pliocene appearance of a purple-black external calcitic layer in *Prisogaster* is an odd event that nonetheless is repeated in western South American *Diloma* Philippi, 1845 (Marincovich, 1973; Nielsen, 2003). The significance of these purple-black outer layers in Quaternary turbinids and western South American trochids [Miocene-Pliocene undescribed species of *Tegula* (*Chlo-*

rostoma) Swainson, 1840; *Tegula* (*Chlorostoma*) *atra* (Lesson, 1830); *T.* (*C.*) *luctuosa* (d'Orbigny, 1841); *T.* (*C.*) *tridentata* (Potiez and Michaud, 1838); and, incipiently, in *T.* (*C.*) *quadricostata* (Gray, 1828)], as well as trochoids from mid- and high-latitude northern Pacific and South African shorelines, merits further investigation.

Occurrences of most modern and Pleistocene specimens of *Prisogaster niger* are consistent with a high-energy intertidal and shallow subtidal habitat with rock-and-gravel substrates (e.g., DeVries collection, Recent, juveniles, eight meters deep, northern Chile; DV 720-1, Holocene, gravel beach ridge, northern Peru; DV 1629-1, upper Pliocene, 250 m marine terrace, southern Peru). The same is true for upper Pliocene occurrences of specimens of *P. valenciai*, which are found in bioclastic coarse-grained sandstones and gravel deposited within 150 meters of a mountainous paleo-shoreline. In contrast, specimens of the older *P. mcleani* are found in well-sorted hummocky cross-bedded sandstones with shell banks of large venerid bivalves, as well as bioclastic sandy gravels, suggesting that the habitat of the late Miocene-early Pliocene species also included foreshore environments with lower energies than typical for intertidal environments.

The late Pliocene was a time of morphological novelty for Mio-Pliocene taxa in Peru other than *Prisogaster*: *Acanthina* Fischer von Waldheim, 1807 (DeVries, 2003), *Concholepas* Lamarck, 1799 (DeVries, 2000), *Xanthochorus* Fischer, 1884 (DeVries, 2005a), and *Tegula* Lesson, 1835 (DeVries, unpublished data). It was during this time that the molluscan fauna of the Mio-Pliocene Peruvian Faunal Province was undergoing the second phase of a local species-level mass extinction (DeVries, 2001) that coincided or at least overlapped with increased rates of tectonic uplift in northern and southern Peru (DeVries, 1986, 1988; Ortlieb et al., 1995) and the transport of greater quantities of gravel and rounded cobbles of Andean andesitic rock to the southern Peruvian coast (DeVries, 2003).

CONCLUSION

With the discovery of two new fossil species in southern Peru, the "enigmatic" turbinid *Prisogaster* now has a pedigree extending back to the middle late Miocene. Miocene and early Pliocene specimens with turbinine features suggest *Prisogaster* did arise from a middle Miocene species of *Turbo*, a possibility raised by Hickman and McLean (1990). The place from which *Prisogaster* or its turbinine ancestor immigrated is uncertain, but based on some similarity in key characters with some species of *Turbo* (*Marmarostoma*), the Indo-Pacific region seems as likely as the Magellanic or Panamic regions. The *Prisogaster* shell underwent a rapid transformation during the late Pliocene, including an axial compression, a streamlining of sutural contacts, a thickening of the shell, a broadening and smoothing of primary spiral cords, and the development of a purple-black outer shell layer. Some of these changes might be construed to have improved the strength of *Prisogaster* shells to more successfully withstand attacks from clawed predators, which seem to have been a common hazard for individuals of *P. mcleani* (see Figures 20, 24, 30, 31). Alternatively, a stronger and more stable shell may have enabled individuals of *P. niger* to survive on rockier, higher-energy, intertidal substrates. Such environments became the norm for coastal Peru when much of the coast commenced a 200 m uplift during the latest Pliocene and protected embayments became fewer and much smaller (DeVries, 2001).

ACKNOWLEDGMENTS

I would like to thank M. Urbina, R. Salas, and M. Stucchi of the Departamento de Paleontología de Vertebrados, Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, in Lima, Peru, for their hospitality and help in the laboratory and field. Helpful suggestions for improving the manuscript were offered by C. Hickman and S. Nielsen. Support for field research was provided in part by a Fulbright scholarship in 1999.

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APPENDIX

Locality-samples:

DV 380-2 Sacaco, in cross-bedded sandstones just below farmhouse, 15°32′29″ S, 74°43′53″ W (Acarí 1: 100,000 quadrangle), Lower Pliocene.

DV 398-1 Playa Canastones, Bahía de la Independencia, Peru (Punta Grande 1:100,000 quadrangle), Recent.

DV 423-1 Terrace deposit capping Miocene strata west of Quebrada Huaricangana, 14°55′29″ S, 75°17′54″ W (Palpa 1:100,000 quadrangle), Pliocene.

DV 160-1 Roadcut along Panamerican Highway, de-

scent from north into Yanca. Shell beds, 15°39′49″ S, 74°31′50″ W (Yanca 1:100,000 quadrangle), Lower Pliocene (same as DV 1598-1).

DV 461-1 Highest marine terrace about five km north of Chala, Peru, uppermost Pliocene/lowermost Pleistocene.

DV 463-1 Lower terrace, 5 km north of Chala (Chala 1:100,000 quadrangle), upper Pleistocene.

DV 464-1 Mid-level marine terrace, five km north of Chala (Chala 1:100,000 quadrangle), middle Pleistocene.

DV 571-1 Alto Grande, about one km south of intersection with abandoned paved road to San Juan de Marcona, on south-facing hillside west of Panamerican Highway; one of several shell banks, 15°26′57″ S, 74°52′06″ W (Acarí 1:100,000 quadrangle), middle upper Miocene.

DV 573-1 Sacaco, shell banks and cross-bedded sandstone just below level of farmhouse (Acarí 1:100,000 quadrangle), lower Pliocene.

DV 720-1 Eastern major cobble ridge near Santa paleo-lagoon, northern Peru (see DeVries and Wells, 1990), Holocene.

DV 730-1 Between Ceros Pimenco and Mentiroso, month of Santa paleo-lagoon, northern Peru (see DeVries and Wells, 1990), Holocene.

DV 806-1 Southwest of Quebrada Usnaca, about 1.7 km west of Hacienda Tunga building, in middle of small natural amphitheater in hillside, highest shell bed. (Palpa 1:100,000 quadrangle), lower Pliocene.

DV 1029-1 Yauca Depression, west of Panamerican Highway, 15°39′29″ S, 75°35′08″ W (GPS, Yanca 1:100,000 quadrangle). lower Pliocene.

DV 1031-1 Section along Panamerican Highway, Quebrada Huambo, about ten km west-northwest of Chala. Roadcut along Panamerican Highway, north face. 15°48′41″ S, 74°21′18″ W (GPS; Chala 1:100,000 quadrangle). Uppermost Pliocene / lowermost Pleistocene. [Note: This locality was mistakenly referred to as Morro Abra de los Chaparrinos (the "Huacllaco section" of DV 1254) in DeVries (2005a, b).]

DV 1252-1 Quebrada de la Vaca, roadcut along Panamerican Highway, south of south wall, uppermost terrace above non-marine deposits, 15°48′56″ S, 74°18′50″ W (GPS; Chala 1:100,000 quadrangle), uppermost Pliocene.

DV 1254-Bal 6 Section along Panamerican Highway, ten km southeast of Chala and above Playa Huacllaco. 35 meters above basement rocks in measured section (see Figure 3), 15°53′25″ S, 74°09′52″ W (GPS; Chala 1:100,000 quadrangle), upper lower Pliocene.

DV 1254-Bal 8 Section along Panamerican Highway, ten km southeast of Chala and above Playa Huacllaco. 42 meters above basement rocks in measured section (see Figure 3). 15°53′25″ S, 74°09′52″ W (GPS; Chala 1:100,000 quadrangle). Upper Pliocene.

DV 1254-Bal 10 Section along Panamerican Highway, ten km southeast of Chala and above Playa Huacllaco. 47.5 meters above basement rocks in measured section (see Figure 3), 15°53′25″ S, 74°09′52″ W (GPS; Chala 1:100,000 quadrangle), upper Pliocene.

DV 1598-1 Roadcut along Panamerican Highway, descent from north into Yauca. Shell beds. 15°39′49″ S, 74°31′50″ W (Yanca 1:100,000 quadrangle), lower Pliocene.

DV 1629-1 Section above Playa Huacllaco, ten km southeast of Chala, uppermost coquina beds (Unit IV; see Figure 3), 15°52′47″ S, 74°10′13″ W (GPS; Chala 1:100,000 quadrangle). Uppermost Pliocene/lowermost Pleistocene.

DV 1635-1 Yauca Depression, west of Panamerican Highway. 15°39′33″ S, 75°34′54″ W (GPS, Yanca 1:100,000 quadrangle), lower Pliocene.